

Laboratory of General Parasitology, Department of Parasitology, Polish Academy of Sciences
Head of Department: Prof. Dr. Witold Stefański
Head of Laboratory: Prof. Dr. Włodzimierz Michajłow

Alicja GUTTOWA

Experimental investigations on the systems
„procercoids of *Diphyllbothrium latum* (L.) — *Copepoda*“

Eksperymentalne badania nad układami
„procerkoidy *Diphyllbothrium latum* (L.) — *Copepoda*“

The problems of mutual correlations between the two components of the „parasite — host” system are in the sphere of parasitology relatively little studied. These problems were studied: in Poland by Michajłow 1932, 1938, 1953, 1959 and Kisielewska 1957, 1957a, 1957b, 1959, in the Soviet Union by Davtian et Šulc 1954, in the U.S.A. by Christian et Alkin 1944 and partly by Humes 1950. An interesting position is the work of Schurmans-Steckhoven 1955, which deals with the problems of morphological and physiological adaptations of parasites. The author devotes considerable attention to the considerations of the mutual correlations between the parasites of various groups and their hosts.

Michajłow's studies referred to intermediate hosts, relations in populations and mutual correlations in systems „procercoids of *Triaenophorus lucii* (Müll.) — *Copepoda*“, Kisielewska worked on similar problems concerning *Drepanidotaenia lanceolata* (Bloch) in Poland. The cited authors offered their own concepts of the classification of the hosts (Michajłow 1932) and of the types of systems (Kisielewska 1959). A general scheme of the classification of the forms of relations between a parasite and a host was presented on the basis of theoretical considerations by Davtian et Šulc 1954.

As regards *Diphyllbothrium latum* the problem of the system „parasite — host” was so far not studied in detail. Beside the works of Pavlovskij et Gnezdilov 1950 on the mutual correlations in the populations of the adult individuals parasitizing dogs, beside the work of Michajłow et Wierzbicka 1935 and that of Humes 1950 on the hosts of procercoids, which include also an attempt to classify them, there is no work dealing in detail with the problems of the system „parasite — host” on any of the sections of the life cycle of this tapeworm. Therefore it seems that a supplement of our informations on this theme is necessary, the more so, as the fish tapeworm is widely distributed in some geographical regions and causes serious losses.

The present work is devoted to the group of problems concerning the formation and development of the parasitological systems which include procercoids of *Diphyllbothrium latum* and their hosts, *Copepoda*.

The investigations included studies on (1) The influence of the external environment on the embryonic development, vitality and invasiveness of coracidia, as the factors which play a very essential part in the process of the formation of the systems; (2) The relations in the populations of procercoids in the systems of various types; (3) The occurrence of the hosts of *D. latum* in the *Copepoda* fauna in Poland and some other countries in the Baltic zone, their classification, variability of the properties of the hosts depending on the factors of the external environment.

All the mentioned studies were conducted experimentally, because under natural conditions it is extremely rarely possible to encounter such a mass contact of the parasites with the hosts to obtain sufficiently high numbers for the statistical calculations. Because of the want of the mass material, the studies under natural conditions permit only to state, on the basis of the presence of larva and the degree of the advance of its development, whether the given species can be regarded as the host, or not. It is evident that the results of the experimental studies reveal mainly the physiological aspect of the problem and illustrate only the potential possibilities of the given species as the host in the field. Under natural conditions, however, very often the ecological factor may gain preponderance. Therefore it seems necessary that, as far as possible, the data collected experimentally should be confronted with the data gained under natural conditions.

I should like to express my indebtedness to Prof. Dr. W. Michajłow for the assistance shown to me for many years in the course of my studies.

I owe also grateful acknowledgement to Doctors M. N. Dubinina and I. E. Bychovskaja-Pavlovskaja of the Zoological Institute of the Academy of Sciences of the U.S.S.R. in Leningrad, and to Dr. R. Vik of the Zoological Institute of the University in Oslo, for their valuable assistance offered to me in the collection of this material and the organization of the studies in the Leningrad zone and in Norway.

Material and methods

The present work was conducted in the period extending from May, 1956 till May, 1960. The experimental studies were conducted at the Department of Parasitology, Polish Academy of Sciences, a part of the experiments was carried on at the parasitological laboratory of the Academy of Sciences of the U.S.S.R. in Leningrad and at the parasitological laboratory of the Zoological Institute of the University in Oslo.

The eggs of the tapeworm were obtained from the II Clinic of Internal Diseases of the Medical Academy in Warsaw and from the anthelmintic centres in Leningrad. From Leningrad the eggs of *D. latum* were transported in test tubes in which the water was changed every several hours.

The material used for the studies on the first intermediate hosts (plankton *Copepoda*) originated from heterogeneous bodies of water (lakes, river pools, ponds, channels) in Poland and from the neighbourhood of the Gulf of Finland and from the lakes of Central and North Norway (Mjösa, Pasvik).

26 species of *Copepoda* were used; this number includes 6 species of *Diaptomidae* and 20 species of *Cyclopidae*.

To study the influence of the temperature on the embryonic development I have placed the eggs into Petri dishes containing water in various temperatures; every day observations were carried on in every culture.

To study the survival of eggs and coracidia under freezing conditions I kept the cultures of eggs in a refrigerator at various temperatures. After a definite period of time the cultures were placed again at room temperature and following thawing

they were examined several days later for their vitality; calculations were made on the basis of the mortality rate of the embryos in the individual cultures.

The studies on the invasiveness and vitality of larvae were conducted immediately following the hatching and at later terms, as well as after the sedimentation of larvae on the bottom of the dish. The test of the invasiveness of larvae required a special method in view of the necessity to select from the population the individuals hatched not later than one hour before. To gain this purpose I selected by use of a pipette eggs that were likely to hatch at the shortest time and I placed them in a minute quantity of water on a slide or watch glass. Into such microcultures I introduced the copepods and tested every few minutes the course of the hatching and the result of the contact of coracidia with the copepods.

To study the influence of the temperature on the invasiveness of the hatching larvae I conducted observations of the larvae in cultures developing at the temperature 8—10°C and 15°C. The invasiveness of the larvae was tested by using the method of contacting them with the hosts and calculating the mean intensity of invasion of the obligatory hosts with the larvae from the individual cultures.

To conduct accurate observations on the development of the populations of the larvae in the body cavity of the hosts I maintained separate cultures of the following invaded copepods: 201 *Eudiaptomus coeruleus* v. *vulgaris* (Schmeil), 249 *Eudiaptomus gracilis* (Sars), 57 *Acanthodiptomus denticornis* Wierzejski, 98 *Cyclops strenuus* Fischer, and 22 *Cyclops insignis* Claus.

In the individual cultures single invaded individuals were isolated into separate dishes what enabled to observe the same specimen several times at definite time intervals. When the shells were transparent, the observations were made without the use of a cover glass in order not to expose the copepode to an injury. Under conditions of more difficult observations the copepode was placed on a slide in a large drop of water and delicately covered with a thin cover glass. Water from an aquarium or from a body of water was used for the individual cultures. The water was changed every day. Some specimens were supplied with additional food, consisting of protozoans specially cultured to this purpose.

3211 *Copepoda* contacted with coracidia were examined. The number included 684 individuals cultured individually and 2527 specimens originated from mass cultures which served partially as the statistical material for the calculation of the intensity and extensiveness of invasion, and partly for testing the invasiveness of the larvae. This number included also not invaded individuals of all the examined species of *Copepoda*.

The eggs were pressed out of the mature segments of *D. latum*, washed and placed in water. The hatching coracidia were every day poured off and brought in touch with the copepods after 24, 48 and 72 hours to test their invasiveness at various age. The cultures of eggs under laboratory conditions (temperature 18—20°C) served not only for the studies of the normal course of the development of *D. latum* but were used also as controls of the results obtained in the studies on the influence of the temperature and light on the development and hatching of coracidia. Therefore every series of the experiments was accompanied by a parallel control culture.

The contact of *Copepoda* with the coracidia took place in glass vessels containing water with the larvae. Depending on the aim of the experiment the contact was maintained for 10—180 minutes. Next the cyclops were transferred to a vessel with pure water and the examination of their intestine and body cavity followed. When the shell of the cyclops was transparent the observations were conducted without the destruction of the animal, but in some cases there was the necessity to press out the intestinal contents to examine the larvae.

The results of the observations concerning the hatching and the degree of the invasion were expressed numerically. To calculate the percentage of the hatched larvae, the empty egg shells and the eggs were counted in 10 microscopic fields, and the mean value of hatching for the whole culture was established (Guttowa 1955—56). The extensiveness of invasion related to one species of the host was obtained from the proportion of the number of the invaded individuals to the total number of the individuals contacted with the coracidia in the given experiment. The term intensity of invasion (the number of individuals parasitizing the organism of the host) applies only to the concrete individual host, therefore in the present paper

for every species of the hosts there are given the numerical data which define the fluctuations of the intensivity occurring in the individuals in the given culture contacted with the larvae. The mean arithmetical value of the intensivity of invasion is also presented.

A very essential problem constitutes the invasiveness of the larvae in the collective sense — as a population (population here — is a conventional term substituting a collection of larvae in one individual host). The individual invasiveness, as a state in which the larva is able to invade efficiently the host, is not a new problem. In the studies so far conducted mainly the invasiveness of the separate individuals was taken into consideration, and the ability of invasion, if any, was stated. Knowing the conditions of the development of the larvae it was possible to conclude whether they would cause the appearance or disappearance of the invasiveness. In the populations of the larvae, the influence of the external conditions can be marked in a more differentiated way. Owing to the individual variability of the larvae there may take place, e. g., a minor or major decrease of the degree of the power of invasion of the given population of the larvae as a whole. This takes place when we study the influence of the temperature, atmospheric pressure or other agents of the external environment on the development of the larvae. Accepting the assumption that the invasiveness of the various populations can be various, I established the conditions at which the extensiveness and the intensity of invasion of the obligatory host is the highest, what proves a high degree of invasiveness of the populations of the larvae. Such conditions are fulfilled by a control culture, it is by a culture kept at the temperature of 18—20°C. The method of calculation the coefficient of the invasiveness of each examined population is described in a separate paper (Guttowa 1955—56). The treatment of the invasiveness as a characteristic of a population is a new approachment and may be useful in studies on the influence of the environmental factors on the invasiveness of the larvae.

I. Influence of external factors on the embryonic development, viability and invasiveness of coracidia of *D. latum*

1. Embryonic development of coracidia at the optimal temperature (18—20°C)

The temperature of 18—20°C is regarded by many authors as the optimal one for the development of eggs of *D. latum* (Neymin 1952, Fedorov 1956, Morozova 1956). Under such conditions I maintained the majority of the cultures. On the 3rd or 4th day after the culture was prepared in the interior of the eggs a central brightening, at the beginning of indistinctly marked outlines, started to appear. On the 5th or 6th day it was possible to observe a distinctly shaped oval form of the oncosphere surrounded by yolk cells of the eggs. On the 8th or 9th day of the development the hatching begun, initially of single individuals. In the course of the next successive days of hatching its intensity gradually increased reaching the culmination point most commonly on the third day from the beginning of the hatching. On the 5th or 7th day there was a gradual decrease of the intensity till the complete termination of the hatching. The percentage of the hatching larvae under the described conditions reached on the average the number 75 — 95.

The hatching took place by the access of light which is an indispensable stimulus to this act (Essex 1927, Thomas 1930, Neymin 1952, Morozova 1957). The withholding of the access of light does not act on the developmental processes. In darkness the embryo develops normally till the moment of the hatching, then the larvae survive within the interior of the egg membranes about 3—4 weeks and finally die. Under the influence of light a mass and violent hatching of all the developed larvae takes place.

2. Embryonic development of coracidia depending on the temperature

A number of egg cultures was kept at the temperatures of 0—2°C, 5—6°C, 8—10°C, 15°C, 18—20°C (control culture), 25°C, 30°C, 35°C. I observed the following parametres: time of the embryonic development, percentage of the survival of the embryos, extensiveness and intensity of invasion of obligatory hosts with larvae from the separate cultures.

The numerical values of the separate observations are presented in the Tables I—IV. As can be seen, the development of the coracidia can take place at the temperature from 8°C to 30°C. Below 8°C no development takes place. In eggs placed in a refrigerator at the temperature of 0—2°C I did not observe any developmental changes for many months, although their viability was maintained to a high degree. These relations are represented in the Table II.

Table I

Influence of temperature on the time
of embryonal development of coracidia
and on percentage of hatching of larvae

Temperature	Time of embryonal development (days)	% of hatching
0-2°C	-	-
5-6°C	-	-
8-10°C	39-42	96
15°C	18-20	96
18-20°C	8-9	96
25°C	7	68-75
30°C	6	41
35°C	-	0

Table II

Influence of cooling on percentage of mortality of *D. latum* embryos

Temperature	0 - 2°C							
Time of cooling (months)	1	2	3	4	5	6	7	8
% of mortality of embryos	4	4	20	15	20	50	50	50

Table III

Percentage of surviving embryos of *D. latum* in relation to temperature and time of freezing

Freezing time Temperature	% of survived embryos						
	hours			days			
	1	3	5	1	2	3	3-10
- 2°C	96	96	96	85	80	70	70-0
- 5°C	41	43	40	3.5	1	0	
- 8°C	48	20	3	0			
- 10°C	10	0					

Table IV

Influence of temperature in the period of development of embryo on the vitality and invasiveness of hatched larvae

Temperature of culture	Longevity of coracidia (hours)	Extensiveness of invasion	Mean intensity of invasion	Invasiveness of population %
0-2°C	-	-	-	-
5-6°C	-	-	-	-
8-10°C	72	92	4.4	100
15°C	48-72	96	3.9	89
18-20°C	48	96	4.4	100
25°C	24-36	74	4.2	95
30°C	12-24	75	3.6	82
35°C	-	-	-	-

As evident from the described observations, low temperatures act negatively on the percentage of the hatching in a mild and longlasting way, high temperatures, however, decrease it violently and to a considerable degree, what is illustrated in the Diagram 1a.

The temperature influences also the time of the embryonic development of the larvae. As shown in the diagram 1b, the embryonic development at the

lowest tolerated temperature (8°C) lasts about 40 days, at the upper thermic limit only 6 days. At the temperature lower than 8°C the development processes are inhibited to the minimum, and stopped at the temperature of 0°C ; however, it does not cause immediate death of the embryos. Above 30°C ,

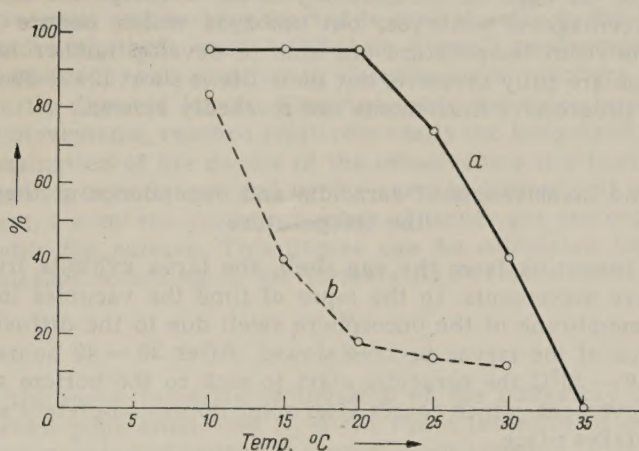


Diagram 1. a — Decrease of percentage of hatching by the increase of temperature of culture; b — Influence of increase of temperature on the time of development

however, the immediate vacuolization of eggs takes place and the death of embryos follows. On the basis of the described data it is possible to discern three temperature limits: temperatures at which the potential possibility of the development is preserved for a long period of time ($0 - 8^{\circ}\text{C}$); temperatures at which the development can take place ($8 - 30^{\circ}\text{C}$); stop of the life processes, lethal temperatures ($30 - 35^{\circ}\text{C}$).

3. Influence of freezing on the survival of embryos

The reaction of embryos to freezing was studied at the temperatures: -2°C , -5°C , -8°C , -10°C . Eggs were deformed to a minor or major degree, but after the thawing they recovered their original shape and in the majority they become vacuolized. In the course of the freezing at -5°C , lasting above 5 hours, the structure of the eggs was permanently damaged. The influence of the temperatures below zero on the percentage of the survival of the eggs is illustrated by the data shown in the Table III.

These data show that at the temperature of -2°C the eggs preserve the ability for farther development for above 10 days, at the temperature of -5°C up to 5 hours; below -8°C the temperatures are lethal.

The resistance of the eggs to freezing is variable and depends to a major degree on the advancement of the embryonic development. In the initial period of the development the embryos endure freezing more easily, but in the course of the developmental process the resistance gradually diminishes. For example,

the embryos on the 1st or 2nd day of the development endure the temperature of -1.5°C for 17 days, but on the 8th or 9th day they die at this temperature in 7 days. After leaving eggs the coracidia die very rapidly at the temperature below zero. Their resistance of freezing is minimal, because at the temperature of -2°C after 3 hours of freezing all the larvae were deformed and burst. The freezing of the eggs on the first day of the development causes death of a certain percentage of embryos, but embryos which endure it, after the transfer to the room temperature are able to develop farther normally. The hatching larvae are fully invasive, but their life is short (24 — 30 hours). Their whirling and progressive movements are markedly slower.

4. Viability and invasiveness of coracidia and dependence of these factors on the temperature

After the liberation from the egg shell, the larva exhibits lively whirling and progressive movements. In the lapse of time the vacuoles in the cells of the external membrane of the oncosphere swell due to the diffusion of water. The movements of the larvae become slower. After 36 — 48 hours at the temperature of $18 - 20^{\circ}\text{C}$ the coracidia start to sink to the bottom showing only a vibrating movement, which ceases after some hours completely and the death of the larvae takes place.

It happens that the larvae ultimately shaped morphologically are deprived of the property of invasiveness. It is the case, e. g., with the larvae of *Triaenophorus lucii* (Guttowa 1955) exposed to long lasting low temperatures ($0 - 2^{\circ}\text{C}$) in the embryonic period. On a number of specimens of various age I traced the phenomenon at what a period of life the larva becomes invasive and when this property disappears in it. Immediately after leaving the egg shell, the coracidia which show a very lively whirling movement proved to be completely invasive. Following the contact with the obligatory host, the larvae were observed densely in the interior part of the alimentary tract. Due to the action of the digestive enzymes the oncospheres were in a short time liberated from the external membranes. Next, using their hooks they inserted themselves in the intestinal walls and started to penetrate towards the body cavity. After several minutes it was possible to observe already the first oncospheres on the external wall of the intestine. Young, lively individuals, cultured at the temperature of $15 - 20^{\circ}\text{C}$ rapidly and massively penetrate the intestinal wall. These symptoms indicate to a high degree of invasiveness of the whole population. If the larvae die in the obligatory host and become digested, their hooks are discharged and in such a case we are dealing with a lack of invasiveness in a major or minor number of the larvae, or with a diminishing of the invasiveness of the whole examined population. In the cultures of larvae kept at the room temperature ($18 - 20^{\circ}\text{C}$) the high degree of invasiveness was maintained on the average for 36 — 48 hours. In cultures kept at lower temperatures ($10 - 15^{\circ}\text{C}$) the invasiveness of the larvae was extended to 72 — 96 hours and lasted on the whole for so long as the whirling and progressive movements were maintained. The larvae which sunk to the bottom exhibited, beside the subsiding of the manifestations of life (slower movements of the hooks and

ciliae), a considerable diminishing of the invasiveness. This entitles to the supposition that not the absolute age of the larvae is a decisive factor of their invasiveness.

The results of the experiments seem to indicate that the invasiveness is maintained as long as the movements of the larvae are preserved. In some control populations the young larvae (24 hours) were already losing their vibrating movement and rocking started to sink slightly to the bottom. *Copepoda* contacted with them were invaded in a small percentage but in their intestinal contents it was possible to observe large numbers of embryonic hooks and partly digested larvae. Simultaneously the older larvae (72 hours), but of lively movements, reached relatively easily the body cavity of the hosts.

The determination of the degree of the invasiveness is a fairly complicated problem. This degree is determined by the average intensity of invasion of the obligatory host, i. e. by the average number of larvae per one copepod brought in contact with the culture. This degree can be calculated for every other studied population according to the formula (Guttowa 1955—56):

$$I = \frac{S_e}{S_c}$$

where S_e is the mean intensity of invasion of the obligatory host contacted with the studied population, and S_c is the mean intensity of invasion of the obligatory hosts contacted with the control population.

The proportion $\frac{S_e}{S_c}$ is an index of the invasiveness of the studied population; $\frac{S_e}{S_c} \cdot 100$ gives the percentage of the invasiveness of the studied population (Table IV).

Summarizing the results it can be stated that the cultures kept under the most favourable conditions (temperature of 18—20°C) are characterized by a uniform and normal development of the embryos, high percentage of the hatching and a normal, as regards invasiveness, population of the hatching larvae.

The processes of the embryonic development lead to the formation of larvae. The vitality and invasiveness of such larvae, as shown by observations, depend also to a minor or major degree on the conditions under which they were developing (Table IV). The temperature, as the most strongly acting environmental factor in the early developmental stages of *D. latum*, reflects markedly on the span of life of the coracidia, whereby lower temperatures prolong the period of life and the invasiveness of the larvae. As shown by the numerical data in the Table IV, the percentages of the invasiveness of the populations of the larvae cultured at temperatures 8°—10°C, 15°C, 18°—20°C and 25°C fundamentally do not differ seriously and the small deviations do not point to the dependence of the degree of the invasiveness on the temperature. Therefore it is possible to risk the supposition that the temperature acts in the embryonic period only on the time duration of the invasive properties of the larvae, but not on the appearance of the invasiveness. Therefore the normally shaped larvae are all in the state of invasiveness.

5. Discussion

Summarizing the results of the described experiments it is possible to draw the conclusion that the development of the embryo of *D. latum* depends to a high degree on the factors of the external environment in which the role of the temperature seems to be the most serious. The temperature of the water, among other factors, defines the optimal conditions for the development of the embryo.

Such conditions are fulfilled to *D. latum* by the temperature of 18 — 20°C. In comparison with the optimal temperature for the development of some parasitic trematodes or nematodes it is rather low.

The results of studies of Neymin 1952, Fedorov 1956, Morozova 1956, 1957 corroborate the general rule that the lower the temperature within the admissible limits, the slower is the course of the developmental processes and the longer are preserved the vital activities of the hatched larvae. After Morozova 1957, the longest span of life of the coracidia (96 hours) is at the temperature of 5°C, the shortest — at the temperature above 25°C. This is undoubtedly connected with the increase of the metabolism and the accelerated processes of diffusion of water from the environment. There is, however, a certain border line to these temperatures below which the eggs of *D. latum* do not develop, but they do not lose their ability for further development. Morozova corroborates these observations. She had placed on the bottom of the lake Onega the eggs of *D. latum* in test tubes without bottom, sealed at both ends with mill gauze and found that the eggs persist at a state of rest during the whole winter and start their development at the beginning of summer. It can be generally stated that low temperatures do not exert a noxious effect on the embryos of *D. latum* provided that the time of the cooling would not exceed 6 months. Longer periods of cooling will cause a gradual increase of the percentage of mortality of the embryos. The results of my studies and Morozova's 1957 data are not in agreement with the observations of Fedorov 1956, who reports that the percentage of the hatching of eggs in cultures kept at the temperature of 2 — 6°C diminishes to one half after 16 days of cooling, and after 30 days of cooling all the eggs die. It might be possible that in the experiments conducted by the quoted author some other environmental factor acted in a noxious way.

Comparing the described data with those referring to *Triacnophorus lucii*, striking is the greater susceptibility of the embryos of *T. lucii* to the temperature below 4°C, expressed by a mortality rate reaching up to 100% after 42 days of cooling at the temperature of 0 — 2°C. The low temperature influences also markedly the degree of the invasiveness of the population of the larvae, which diminishes to 66% in cultures kept at lower temperatures than 4°C. *T. lucii* shows a considerably more marked thermic specificity, expressed by an immense increase of the mortality of the embryos at the temperature below 4°C.

Drepanidotaenia lanceolata reacts in a milder way to low temperatures. Kisielewska 1957 found that the temperature of 2 — 4°C favours longer survival of live and invasive eggs and that the diminishing of the invasive power of the eggs is at this temperature mild and gradual. The lethal temperatures are below 1°C and above 34°C.

Interesting is the phenomenon of a better adaptation of *D. latum* in the first developmental stages to lower than higher temperatures. This is accomplished by the inhibition of the developmental processes without the loss of further possibilities in this direction, or owing to the considerable resistance to freezing. These properties of *D. latum* can considerably facilitate the survival under conditions reigning in the zone of its occurrence. In Europe the area of its occurrence is mainly the Baltic zone and the terrains located north of it, characterized by a cool climate. The resistance to low temperatures may be an expression of the evolutionary fixed adaptation of this species to the living conditions.

II. Influence of the environment of the I order on the origin of the systems „*D. latum* — Copepoda”

1. Development of the proceroids in the obligatory host

Following the penetration of the oncosphere through the intestinal wall to the body cavity of the host there begins its transformation into a proceroid. The diameter of the oncosphere at this moment is on the average 38.8 μ . In the first period of the development the larvae are located mainly on the surface of the intestine and together with its movements they advance towards the interior of the body cavity. I never observed the larvae in the abdomen, furca or antennae. At the temperature of 18 — 20°C, on the 6th—8th day after invasion, the larva has a slightly elongated shape and is above 200 μ in length. The demarcation of the cercomer begins usually between the 8th and 12th day of the development. Simultaneously the calcareous bodies appear in the parenchyma of the proceroid. On the 14th day after invasion fully developed proceroids can be observed in the body cavity. On the next days the proceroid increases considerably in its size (the mean length of the parasite without the cercomer is 450 — 500 μ). The calcareous bodies become considerably enlarged, the cuticle becomes thicker and the colour of the parasite becomes darker.

Among the hosts studied experimentally in Poland, the leading position is occupied by *Eudiaptomus coeruleus* v. *vulgaris* (Guttowa 1956).

The circle of the auxiliary hosts should be subdivided into two categories.

(1) Species in which the first selective barrier (intestinal juices) acts strongly. These species are characterized by low intensity and extensiveness of invasion.

(2) Species of a mildly acting first selective barrier, but a strongly acting second barrier (conditions reigning in the body cavity of the host). In this case the intensity of invasion is considerable, but the development of the population both of the overdense and not too dense populations has an atypical course. The deviations are most commonly observed in the rate and uniformity of the development of the population.

In my material, the typical representatives of the first category under the Polish conditions are: *Cyclops vicinus* and *C. furcifer*, of the second — *Eudiaptomus gracilis*.

2. Development of population* of proceroids in obligatory host,
Eudiaptomus coeruleus v. *vulgaris*

After a several hours lasting contact of *E. coeruleus* v. *vulgaris* with the coracidia I observed a considerable density of the number of the larvae (10 — 15 individuals).

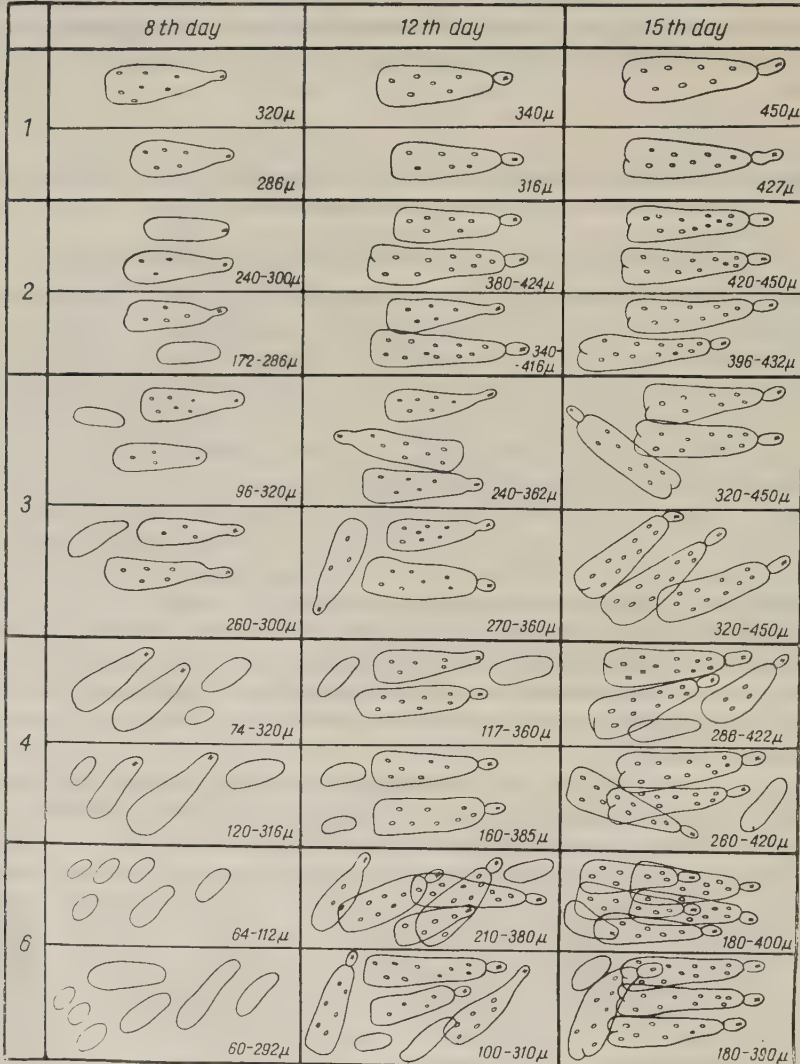


Fig. 1. Variants of situation in 8th, 12th, and 15th day of development of population of *D. latum* proceroids in the obligatory host, *Diaptomus coeruleus* v. *vulgaris*

* The term „population” refers to the ensemble of larvae in the body cavity of one host (Michajłow 1953). A population not overdense consists of 1—3 indivi-

The presence of a considerable number of the proceroids does not influence apparently the vital functions of copepods. The genus *Diaptomus* is a difficult object to culture under laboratory conditions, nevertheless the individuals invaded intensively (10 — 15 larvae) survived on the average over 20 days, and even 6 weeks. These facts prove that the invasion with larvae of *D. latum* does not cause the death of the hosts. In overdense populations I did not observe a diminishing of the number of the larvae, all the individuals attained the proceroid form, and differed only by the size.

I examined 75 populations of various degree of density. In populations not dense the development and growth of the larvae run uniformly. The average length of the proceroids was 350 — 450 μ on the 14th day of the development. All the individuals attain the proceroid form at the same time. The variants of the situations observed on the 8th, 12th and 15th day of the development are schematically represented in the Fig. 1.

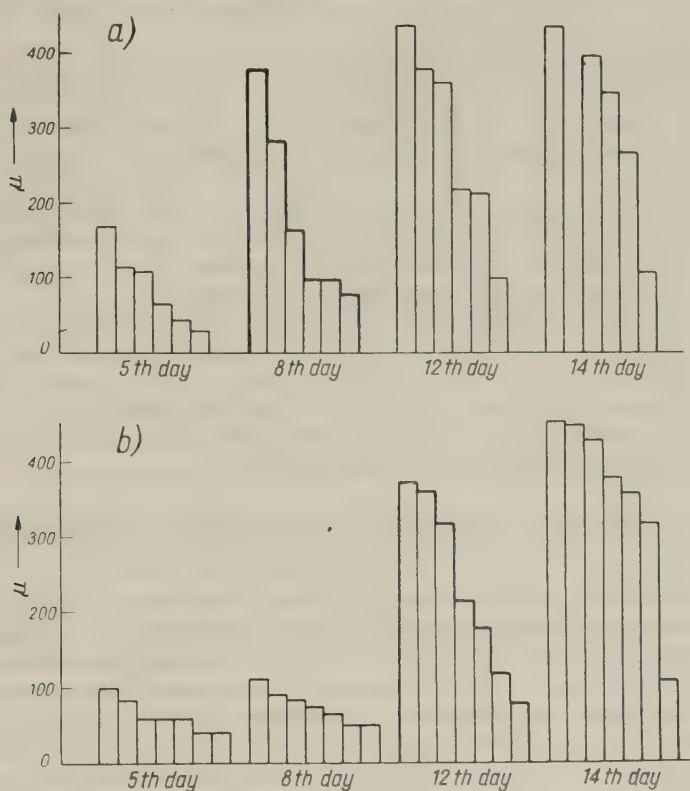


Diagram 2. Growth of specimens in the same population in the 5th, 8th, 12th, and 14th day of its development. A thick line stresses the variability of population as to the growth in the 8th day of its development. a — 6 individuals population; b — 7 individuals population

duals. An overdense population consists of a higher number of individuals. The numerosity of a population depends to a considerable degree on the mass occurrence and time of the contact of the host with the coracidia.

In very dense populations, however, there appeared not an uniform development: a part of the individuals was developing at a normal rate and attained at the defined term the proceroid form, the other part, however, compensated their delay after several days. In very dense populations there occurred also a certain insignificant percentage of larvae strongly inhibited in their development and growth. The mean length of the proceroids was smaller and, e. g., in a population numbering 2 larvae it was on the 14th — 16th day of the development 400 — 450 μ , and in a population consisting of 6 larvae — only 280 — 320 μ . In consequence of this increase in number of the individuals in a population there is a clear diminishing of the maximal dimensions of the proceroids in the populations. The differences in the growth of the larvae become most clearly evident at the moment of the appearance of the first proceroid form, when the population enters into the period of maturation. As the number of the developed proceroids increases, the negative influence of the overdensity on the uniformity of the growth of the whole population becomes less effective.

This phenomenon is best illustrated by the Diagrams 2a and b. The diagrams show that the greatest unevenness of the growth of the individuals in a very dense population occurs on the 8th and 12th day, respectively. In the first period of the development no major deviations in the growth can be observed. Between the 8th — 12th day there appear the first proceroids and the populations become subdivided into three groups: individuals leading in the development, compensating their growth, and strongly delayed. Beginning from the 14th day from the moment of the invasion the curve of the growth of the individuals in the population begins to become even.

As indicated by measurements and observations, the terms of the appearance of the separate changes in the structure under very dense conditions become delayed so much that the first outlines of the typical form of the proceroids appear as late as on the 11th — 12th day following the moment of invasion. The numerosity of a population exerts therefore a clear influence on the rate of the development, causing its delay.

3. Development of population of proceroids in auxiliary host, *C. vicinus* and *C. furcifer*

In auxiliary hosts with a strongly acting first selective barrier we are dealing mainly with a small number of larvae. In *C. vicinus*, the highest intensity of invasion was 9 larvae, in *C. furcifer* — 5 larvae. The mean intensity of invasion in both species was 22.1 larvae per a copepod. In connection with this, the examination of the population relations in this category of hosts will refer only to the not overdense populations.

The growth of the larvae and the rate of their development have a uniform course. The length of the mature proceroids is in both cases about 500 μ . The formation of the cercomer begins on the 10th — 12th day from the moment of invasion. On the 14th day in the majority of the copepods the well developed proceroids could be observed. It is interesting that in this group of hosts I was able to observe several cases of inhibition of the development at its initial stage. This phenomenon occurred in populations of heterogeneous numerosity. There are examples that a population consisting of 4 larvae developed nor-

mally, while the individual larva attained at the same time barely the dimensions three times larger than they had at the moment of the invasion. Such cases, however, are sporadic. The most common type of these relations, as regards the growth and rate of the development, is its correct and regular course.

4. Development of population of proceroids in auxiliary host, *Eudiptomus gracilis*

I have examined 36 not overdense populations in hosts cultured individually. The first significant phenomenon in the intrapopulation relations is the absence of regularity in the growth and development. The dimensions of the solitary proceroids are often smaller than in populations composed of several individuals. The dimensions of the developed proceroids fluctuated within the limits of 340 — 450 μ . Enormous difficulties are rendered in determination of the regularity of the development in time. There are numerous cases where on the same day of the development it is possible to observe in various individuals hosts the larvae of various dimensions (Fig. 2). The larvae greatly delayed in development, which have, e. g., on the 15th day following the invasion 80 — 120 μ in length, show already no tendency of growth in the course of the next days. Most probably, they are already deprived of the chance to attain complete development. This phenomenon could be observed in 30% of the not overdense populations.

The development of the cercomer does not occur before the 8th day from the moment of the invasion, but most commonly on the 10th — 12th day of the development. From the observations and numerical data there emerges a mosaic picture, which does not reflect distinctly the direction of the development of the population of the larvae, what occurs particularly strikingly in comparison with the analogous data for the populations developing in the obligatory host (Fig. 1).

5. Influence of numerosity on the speed of growth and development of a population in auxiliary host, *Eudiptomus gracilis*

I examined the development of 42 overdense populations (4 — 10 larvae) in hosts cultured individually. I found that the degree of the density of a population exerts no influence on the diminishing of the maximal dimensions of the individual larvae. There could be observed distinctly an unevenness of the development (leading individuals, overtaking individuals, and strongly inhibited specimens). The percentage of the latter increased markedly under the conditions of overdensity. Beside the unevenness of the development within a population, which is most probable a phenomenon caused by the mutual interaction of the individuals, there can be observed also an unevenness of the development of the population as a whole in the separate individuals of the same host species (on the same day it is possible to find populations with the developed proceroids and populations little advanced in their development). Hence there results the mosaic picture of the development of larvae of *D. latum* in *E. gracilis* (Fig. 2).

The separation of the cercomer begins on the 8th — 15th day from the moment of the invasion. The numerosity of the population does not play in this case any part. The larvae in populations consisting of 5 individuals can

develop at the same speed as single larvae. This individuality indicates a correlation between the course of the development and the individual characteristics of the host, what may show a poor mutual adaptation of the host and parasite.

6. Dying out of the larvae in the body cavity of hosts

In the course of the studies of the intrapopulation relations I observed the phenomena of delaying, total inhibition of the development or dying out of the larvae. The three phenomena were observed mainly in the body cavity of

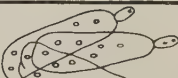
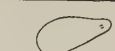
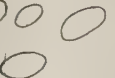
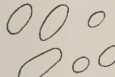
	8th day	12th day	15th day
1	 250 μ	 80 μ	 360 μ
	 115 μ	 240 μ	 80 μ
2	 60-78 μ	 346-360 μ	 96-420 μ
	 110-280 μ	 100-180 μ	 72-78 μ
3	 63-280 μ	 96-340 μ	 352-374 μ
	 90-120 μ	 50-190 μ	 50-112 μ
4	 60-320 μ	 76-240 μ	 85-172 μ
	 60-125 μ	 50-150 μ	 50-440 μ
5-6	 50-110 μ	 75-385 μ	 45-395 μ
	 73-375 μ	 145-380 μ	 72-450 μ

Fig. 2. Variants of situation in 8th, 12th, and 15th day of development of population of *D. latum* procercoids in the auxiliary host, *Eudiaptomus gracilis*

accidental hosts — *C. strenuus strenuus* (in adults and in a certain percentage in copepodits) and *C. insignis*. These pathological manifestations were observed in both species to a various extent. In 22 cases of invasions of *C. insignis*, in 15 individuals there appeared complete degeneration of the population at the initial period of the development. In 7 individuals I observed a slight increase in size, followed by an inhibition of further growth and development of the larvae. In *C. strenuus strenuus* the degeneration was observed barely twice in 19 cases of the invasion. The phenomenon of the inhibition of the development and of the delay of the speed of growth was the dominating form of the intrapopulation relations in this species.

Larvae poorly advanced in their development succumbed exclusively to the dying out. The first symptoms of the degeneration were manifested on the 3rd or 4th day following invasion. In the larvae measuring 35 — 42 μ , there appeared on the about 6th — 8th day of the development a distinct vacuolization. On the external surface of the cuticle there appeared small vesicles containing fluid which gradually disappeared. The larva resembled in this state the form of an egg in the stadium of segmentation. Simultaneously its dimensions gradually diminished. In the final stage of this process the larva became a dark point above which upwards projected or sideways scattered were the hooks. Finally those hooks remained the sole trace of the died larva.

I did not observe any dependence of the dying out of the larvae on the numerosity of the population. It should be added that the dying out was encountered exclusively almost in the accidental hosts, where a low intensity of invasion was observed.

The phenomenon of the dying out of the larvae of the tapeworms in the body cavity in the intermediate hosts was described in the literature. Dubinina 1950 describes the disintegration of the proceroids of *Ligula colymbi* in the body cavity of the obligatory host several days after the complete development of the proceroid. Dubinina explains this phenomenon by the rapid loss of vitality in case the proceroids are unable to reach at the proper time the next host, therefore they die and become disintegrated. The dying out of larvae of *Drepanidotaenia lanceolata* in the body cavity of the intermediate hosts at the various degree of the advancement of the development was observed by Kisielewska 1957. According to the authoress, the mortality of the larvae is connected with the type of the system „parasite — host”. The dying out of the larvae of *D. latum* found exclusively in the group of the accidental hosts corroborates such an interpretation.

7. Inhibition and delay of the development of larvae

The phenomenon of the inhibition of the development of the larvae without the dying out was observed in the accidental system „proceroids of *D. latum* — *C. strenuus strenuus*”. Among the 20 individually cultured invaded specimens, in 8 cases an inhibition of the growth at the dimensions of 40 — 53 μ was recorded. Successive repeated measurements did not show any tendency of growth and such a state was often maintained till the death of the copepod. The numerosity of the population appears not to play in this case a major part. The intensity of invasion was from 1 — 5 larvae, whereby I did not notice differences in the growth and speed of the development of the larvae

in the two different, as regards numerosity, populations. In several cases I observed a progressive and considerably diminished speed of the growth of the larvae (on the 10th day from the moment of the invasion the larvae were 100 — 180 μ in length). To make a comparison it is worthwhile to add that in the course of the normal development in the control cultures the larvae in not overdense populations attain usually on the 10th day of the development about 300 μ in length. As the time passed, the speed of the growth gradually diminished. As a result the developmental changes became more and more difficult to record and in all the examined cases the proceroid was not yet formed on the 25th — 30th day after invasion. The inhibition of the development and the dying out of the larvae was observed in the majority of the cases exclusively in the accidental hosts. Therefore it can be stated that these phenomena are characteristic to a considerable degree to accidental systems of the larvae of *D. latum* — *Copepoda*.

8. Discussion

Both the environment of the I order and the environment of the II order play in the process of the formation of the „host — parasite” system a very important part. A system can arise only under certain conditions. Michajłow 1959 lists the following conditions: (1) a possibility to get in touch and to make mutual contacts between the partners, and (2) factors arising in the course of the contact, defined by the author by the term resistance.

The infestation of the first host by the larvae of *D. latum* is a two-stage process. The first stage is completed by the penetration of the larvae into the body cavity of the host. The second stage is the development of the parasite in the body cavity of the host. The success of an invasion depends on the penetration of the larvae through the intestinal wall into the body cavity. The subsequent fate of the larvae is a matter of mutual relations between the parasite and the host. During the process of invasion of the host a double selection of the larvae can be observed. The set of the selective factors defined as „selective barriers” (Michajłow 1932) is present in the digestive juices of the alimentary tract and limits the survival and invasiveness of the larvae penetrating into the body cavity. It is present also in the fluids of the body cavity which, jointly with the whole set of factors of an immunological and physiological nature, influence the consequent development of the larva. The action of the selective barriers is the basis of the differentiation of the copepods as the potential natural hosts of the proceroids of *D. latum*. The strong action of the first selective barrier causes the digestion and removal of the larvae from the alimentary tract, what limits the degree of the invasion of the host. The second selective barrier is formed by the fluids of the body cavity and its action may express itself by delaying or inhibiting the development, and often it causes the dying out of the larvae.

The fact that some species of *Copepoda* are the obligatory hosts to some species of the tapeworms and other digest their larvae supports the conclusion that the nature of the selective barriers is determined not only by the sole chemical character and activity of the intestinal juices and fluids of the body cavity, but also by the adaptation of the parasites to them.

The influence of overdensity of the parasites on their size and time of the maturation is stressed by Pavlovskij et Gnezdilov 1950 in their work

on the population phenomena in adult individuals of *D. latum* in the final host. Michajłow 1953 and Wiśniewski 1958 draw attention to the differentiation of the structure of a population living under the conditions of overdensity. Generally it is stated that in the overdense populations the phenomenon of the intraspecies competition with a lethal result does not appear. My studies corroborated also these observations that the numerosity is a factor influencing the structure of the population, the speed of the development and the growth of the individual larvae.

A condensation of a population of parasites, limiting the growth and development of a part of the individuals is, according to many authors (Pavlovskij et Gnezdilov 1950, Michajłow 1953, Kisielewska 1957c) a very advantageous phenomenon from the point of view of the preservation of the species. It is an adaptation to the preservation of species under difficult conditions of existence by way of diminishing the growth and inhibiting the development of a part of the individuals, which do not loose the property of further development under more favourable conditions. Because under conditions of small numerosity the development of a population presents an uniform and continuous picture, the question arises what are then the causes of the described population phenomena? At a considerable condensation of a population there is undoubtedly a certain food deficiency, which becomes more acute proportionally to the condensation. It seems probable that the trophic factor modulates in this case the structure of the population and prevents an annihilation of a part of it by limiting the growth and maturation of a certain number of the individuals, most commonly that part which is in a worse situation.

The dying out or the inhibition of the development, observed often in the populations of the procercoids in the non-obligatory hosts, remain probably not in any relation with the described interdependences resulting from the intrapopulation correlations. They appear mainly in hosts characterized by a weak action of the first selective barrier. In this case the invasion of the copepods can take place. A strong action of the second selective barrier inhibits the development or kills the larvae. It seems that two factors may act here in a major or lesser degree: lack of components required by the larvae or presence of noxious agents in the fluid of the body cavity, and the defensive reaction of the hosts. The inhibition of the development or the dying out of the larvae depend on the degree of the action of the described factors. It seems that the source of the described phenomena in the populations of the procercoids of *D. latum* in the accidental hosts is the defensive reaction of the hosts which is the stronger, the lower is the degree of the mutual adaptation between the parasite and the host.

III. System „procercoids of *D. latum* — Copepoda” on the background of ecological and geographical conditions

1. Hosts of the procercoid of *D. latum* in Poland

Positive results of the contact of the copepods with the coracidia in the material from Poland were obtained with 8 species of Copepoda (Table V). These species succumbed to the invasion in a major or lesser degree. I found that *C. strenuus strenuus* was susceptible to invasion only in the phase of the

copepodit in a degree sufficiently high to play the role of a host of this parasite. *Eudiaptomus zachariasii* becomes invaded only sporadically and probably under natural conditions plays no major part. In *C. insignis* there occurs, as a rule, the dying out of the larvae what was also found on a considerably larger material from the Finnish Bay. However, *Eudiaptomus coeruleus* v. *vulgaris*, *E. gracilis*, *C. vicinus* and *C. furcifer* play a certain part in the developmental cycle of *D. latum* in Poland (Table VI).

Out of the four species of hosts, the greatest extensiveness of invasion occurs in *Eudiaptomus coeruleus* v. *vulgaris*. It is a thermophilic form, occurring in spring, summer and early autumn. The season of its occurrence coincides with the period of the embryonic development of *D. latum*, which under natural conditions takes place in spring, summer and autumn. The intensity of invasion attains the highest degree, and the rapid speed of the developmental changes at the temperature of 18—20°C leading to the formation of the proceroid indicate that the most favourable conditions for the development of the parasite are in this phase.

E. gracilis is the characteristic form of the pelagial of large lakes. It occurs most numerous in summer (summer maximum of occurrence — May, September), and in winter (winter maximum of occurrence — November, January). It shows a fairly high percentage of extensiveness of invasion; however, in the speed of the development of the proceroid there occur disturbances and there is a general tendency to delay of developmental changes. Only in young forms a high extensiveness and intensity of invasion can be observed, as well as the quickest speed of development. The young forms of *E. gracilis* fulfil the conditions of the obligatory host of the proceroids of *D. latum* in Poland.

Cyclops vicinus is a characteristic species to the pelagial of lakes, but it is present also in the small bodies of water, particularly in winter and spring. It occurs often together with *C. vicinus* v. *kikuchii*. Both forms become invaded in a fairly high percentage. In the majority of the individuals after some minutes of contact with the coracidia, the intestines were filled with the remnants of the partly digested larvae and their loosely lying hooks in the lumen of the intestines. Usually only a small number of them penetrated to the body cavity, where further development took place normally and rapidly (10—14 days). The data of Michajłow et Wierzbicka 1935 are in disagreement with my findings. The quoted authors recorded a considerable lower extensiveness of invasion in both species and observed also a difference in the susceptibility between *C. vicinus* and *C. vicinus* v. *kikuchii*. According to their data, *C. vicinus* became invaded in a low percentage (2%), while *C. vicinus* v. *kikuchii* showed 12% of extensiveness of invasion.

C. vicinus differs from *E. gracilis* by the very low mean intensity of invasion, what is an evidence of a strong action of the first selective barrier. The proceroids developing in the body cavity attained usually large dimensions (400—500 μ) and were distinguished by a strong motility.

C. furcifer became easily invaded in the spring months (May, June). The extensiveness and intensity of invasion are in this species lower, but the speed of the development of the proceroids and their dimensions indicate to favourable conditions for the development of the parasite.

T a b l e V
Copepoda species becoming invaded in Poland

Species	Specimens		
	contacted	invaded	extensiveness
<i>Eudiaptomus coeruleus</i> v. <i>vulgaris</i> (Schmeil)	243	208	85.2
<i>Eudiaptomus gracilis</i> (Sars)	223	145	64.7
<i>Eudiaptomus zacharisi</i> (Poppe)	10	2	20.0
<i>Cyclops strenuus strenuus</i> Fischer	310	22	7.0
<i>Cyclops strenuus strenuus</i> Fischer (juv.)	28	26	92.0
<i>Cyclops vicinus</i> Ulj.	157	101	61.7
<i>Cyclops vicinus</i> v. <i>kikuchii</i> (Smirn.)	65	32	49.3
<i>Cyclops insignis</i> Claus	7	2	28.6
<i>Cyclops furcifer</i> Claus	71	37	52.1

T a b l e VI
Data on invasion of copepods in Poland

Copepode species		No. of specimens		Extens.	Intens.	Devel. period (days)
		cont.	invad.			
<i>Eudiaptomus coeruleus</i> v. <i>vulgaris</i>	♀♀	148	131	88.5	4.4 (1-22)	8 - 10
	♂♂	94	77	81.9	2.8 (1-5)	10 - 12
<i>Eudiaptomus gracilis</i>	♀♀	134	89	66.4	3.9 (1-11)	various
	♂♂	89	56	63	3.4 (1-13)	various
	juv.	34	34	100	7.7 (5-20)	8 - 10
<i>Cyclops vicinus</i>	♀♀	117	78	66.2	2.0 (1-9)	10 - 14
	♂♂	40	23	57.2	2.2 (1-5)	10 - 14
<i>Cyclops furcifer</i>	♀♀	71	37	52.1	1.6 (1-6)	7 - 8
	♂♂	-	-	-	-	-

2. Classification of hosts of the proceroids of *D. latum* in Poland

The comparison of the characteristics of the quoted four *Copepoda* species suggests a certain scheme of their classification as the hosts of the proceroids. It seems that this scheme fits also to a certain degree with the group classification presented by Michajłow (1932, 1938). Evaluating the role of the individual species of *Copepoda* susceptible to invasion, the author differentiates 5 groups of hosts of the proceroid of some *Pseudophyllidea*. He accepts as the basis of the classification of the first intermediate hosts the extensiveness and intensity of invasion and the speed of the development of the larvae in the body cavity of the host (Michajłow 1938).

In my studies there appear 4 groups of hosts.

(1) Species easily invaded. In several minutes following the contact with the coracidia in their body cavities there are already present the larvae and in the intestine no mass digestion of them is observed. Almost all the contacted individuals become invaded and the development of the proceroid at the temperature of 18 — 20°C lasts about 14 days. This group of hosts should include *Eudiaptomus coeruleus* v. *vulgaris* and the copepodites of *E. gracilis*. In Michajłow's classification these species should be included to the V group. They are obligatory hosts characteristic to this parasite in Poland (Guttowa 1956). These species can also under natural conditions play the main part in the developmental cycle of *D. latum* to such a degree as the ecological relations will permit.

Adult individuals of *E. gracilis*, in view of the high extensiveness and intensity of invasion, fulfil the conditions of the obligatory hosts. However, the prolongating period of the development of the proceroids, inhibition of the development, or various kind of disturbances of its course indicate an insufficient stabilization of the adaptation of *D. latum* to this host species. This characteristic ranks *E. gracilis* to the second place among the obligatory hosts. Under favourable conditions (domination in the plankton of a given terrain) it can play the main part in the developmental cycle of the parasite.

(2) The second type of hosts, corresponding to the IV group of Michajłow's classification, is formed by species marked by a strong action of the first selective barrier. Due to this, the intensity of invasion is low, but the development of the larvae in the body cavity runs without disturbances and at a rapid speed. They are auxiliary hosts and here should be included *C. vicinus*, *C. vicinus* v. *kikuchii*, *C. furcifer*, and the copepodites of *C. strenuus strenuus*.

(3) The third group is formed by *Copepoda* which become invaded accidentally. The proceroids are never formed in them and the larvae die mainly out. In the examined material it is represented by *C. strenuus strenuus* and *C. insignis*. This type of hosts can be included to the III group according to Michajłow's classification.

(4) Finally there remains a long list of species completely resistant to the invasion with *D. latum*. It includes the genera *Macrocyclops*, *Mesocyclops*, *Acanthocyclops*, *Ectocyclops*, *Eucyclops*.

It is characteristic that the four quoted groups can be separated in material collected from various geographical zones.

Thus on the basis of laboratory studies in Poland, the correlations between *D. latum* and *Copepoda* can be represented in the following way:

Obligatory hosts: *Eudiaptomus coeruleus* v. *vulgaris* (Schmeil), *E. gracilis* (Sars) (juv.).

Auxiliary hosts: *E. gracilis* (Sars), *Cyclops vicinus* Ulj., *C. vicinus* v. *kuchii* (Smirn.), *C. furcifer* Claus, *C. strenuus strenuus* Fischer (juv.).

Accidental hosts: *C. strenuus strenuus* Fischer, *C. insignis* Claus, *E. zachariasii* (Poppe).

It should be added that *E. gracilis* (adult forms) does not fulfil in Poland the conditions of an obligatory host because of the distinct disturbances of the development of the proceroids in the body cavity. However, due to the high extensiveness and intensity of invasion and generality of occurrence it can under ecological and geographical conditions of Poland play the main part in the developmental cycle of *D. latum*.

3. Variability of the „host — parasite” systems

Analysing the extensiveness and intensity of invasion of *E. coeruleus* v. *vulgaris*, the attention is drawn to the presence of certain differences connected with the sex of this host (Table IX). The females of this species differ from the males by twofold higher intensity of invasion. Simultaneously there is a more rapid development of the proceroids in the females what proves that there is a certain kind of a physiological sexual dimorphism.

It seems that in *C. strenuus strenuus* and *E. gracilis* there occurs an increase of the resistance of the hosts connected with the age. I observed a far advanced development of the proceroids only in the body cavity of the third and fourth copepodid of *C. strenuus strenuus*. In adult individuals of this species the most common phenomenon was the inhibition of the development, or the degeneration of the larvae. Out of the 256 adult cyclops contacted with the coracidia, only 19 became invaded, whereby in all were observed disturbances of the development of the proceroid. At the same time the copepodids exhibited a high percentage of the extensiveness and intensity of invasion. A similar phenomenon of a resistance to the invasion I observed in *E. gracilis*.

The change of the resistance connected with the age, or sex indicates that the same species of host can play a different role in the developmental cycle of the parasite.

4. Hosts of the proceroids of *D. latum* in the Baltic zone

Studies on the hosts of the proceroids of *D. latum* were conducted on three areas of the Baltic zone: in Poland, in the environs of the Gulf of Finland in the U.S.S.R., and in the south and north of Norway (Fig. 3). Complete list of the examined *Copepoda* is represented in the Table VII. The total number of 26 species of *Copepoda* was examined. The results of the studies conducted in Poland were described in the preceding chapter. The period of the studies conducted on the areas of the Gulf of Finland and in Norway was much shorter and the species occurring seasonally were not studied there.

T a b l e V I I
List of Copepoda investigated in the Baltic zone

No.	Species	Poland	Bay of Finland	Norway	Total
	C y c l o p i d a e				
1	Macrocylops albidus (Jurine)	316	-	72	388
2	" fuscus (Jurine)	83	-	16	99
3	" distinctus (Richard)	-	12	-	12
4	Eucyclops macrurus (Sars)	111	25	17	153
5	" macruroides (Lill.)	46	17	22	85
6	" serrulatus (Fischer)	138	12	35	185
7	Ectocyclops phaleratus (Koch)	3	16	-	19
8	Cyclops strenuus strenuus Fischer	340	34	47	432
9	" vicinus Ulj.	157	37	-	194
10	" vicinus v. kikuchii (Smirn.)	65	-	-	65
11	" abyssorum Sars	72	-	-	72
12	" lacustris Sars	-	-	45	45
13	" scutifer Sars	-	-	56	56
14	" furcifer Claus	71	-	-	71
15	" insignis Claus	7	73	17	97
16	Megacyclops viridis (Jurine)	135	5	21	161
17	Acanthocyclops vernalis (Fischer)	102	-	52	154
18	Diacyclops bicuspidatus (Claus)	24	-	-	24
19	Mesocyclops leuckarti (Claus)	24	12	42	78
20	Thermocyclops oithonoides (Sars)	24	-	33	57
21	" dybowski (Lande)	-	7	-	7
	D i a p t o m i d a e				
1	Hemidiaptomus amblyodon (Marenz.)	17	-	-	17
2	Eudiaptomus gracilis (Sars)	179	115	64	358
3	" graciloides (Lill.)	-	15	-	15
4	" zacharias (Poppe)	10	24	-	34
5	" coeruleus v. vulgaris (Schmeil)	243	-	-	243
6	Acanthodiaptomus denticornis (Wierzejski)	-	-	90	90



Fig. 3. Map of investigation places

On the areas of the Gulf of Finland and in the Leningrad zone I examined 14 species of the local *Copepoda* occurring in autumn. The positive results of the contact of the copepods with the larvae of *D. latum* are represented in the Table VIII.

Table VIII
Extensiveness and intensity of invasion of copepods
of the Bay of Finland with *D. latum*

Species	Extens. of invasion %	Mean intens. of invasion
<i>Cyclops strenuus strenuus</i> Fischer (juv.)	35	2.1
<i>Cyclops vicinus</i> Ulj.	67	3.2
<i>Cyclops insignis</i> Claus	33	1.6
<i>Eudiptomus gracilis</i> (Sars)	97	6.8
<i>Eudiptomus graciloides</i> (Lill.)	100	4.3
<i>Eudiptomus zechariasi</i> (Poppe)	15	1.0

From the criteria accepted in this work it results that the obligatory hosts are *E. gracilis* and *E. graciloides*. Both species are characterized by a very high extensiveness and intensity of invasion. *C. strenuus strenuus* becomes invaded mainly at the stage of the copepodid. The invasion of the adult individuals terminated usually in the dying out, or inhibition of the development of the larvae. *C. insignis* at the low (33%) extensiveness of invasion is characterized by an abnormal course of the development of the larvae in the body cavity.

In south Norway and on the area of the lake Pasvik (Fig. 3), out of the 15 species occurring in spring (May, June) in lakes and small water reservoirs, to the experimental invasion succumbed 5 species (Table IX). Attention deserves the considerable extensiveness and intensity of the two *Diaptomidae* species. It should be added that *Acanthodiaptomus denticornis* is a very common species in various types of water bodies in Norway. Attention is drawn by the fact that the adult forms of *C. strenuus strenuus* became invaded in the described experiments. The extensiveness of invasion reached 44% and in every case the development of the procercoid took place.

T a b l e . IX
Extensiveness and intensity of invasion with *D. latum*
of copepods in Norway

S p e c i e s	Extens. of invasion %	Mean intens. of invasion
<i>Cyclops strenuus strenuus</i> Fischer	44	2.6
<i>Cyclops lacustris</i> Sars	46	2.2
<i>Cyclops scutifer</i> Sars	10	1.3
<i>Eudiaptomus gracilis</i> (Sars)	54	3.0
<i>Acanthodiaptomus denticornis</i> (Wierzejski)	70	3.2

It results from the presented data that the list of the hosts and the extensiveness and intensity of invasion in the three areas of the Baltic zone show certain differences.

Eudiaptomus gracilis examined in all three areas of the Baltic zone shows a clear preponderance as the host of the procercoids of *D. latum* only in the area of the Gulf of Finland (97%). In Poland and Norway the extensiveness of invasion in this species is considerably lower (54 — 65%).

5. Influence of geographical factors on the systems *D. latum* — Copepoda

a. Experimental studies

The comparison of the data from the three various areas of the Baltic zone (Fig. 3) indicates that there is a strong influence of the geographical factors on the relation of the two components in the system „parasite — host”. This

is supported by the differences in the mutual correlations between the examined hosts and *D. latum*. Differences were also found in the course of the cross-invasion of hosts with the parasite from the various areas. In the present experiments I limited the studies exclusively to one host species, *Eudiaptomus gracilis*.

I conducted 4 series of experiments on the invasion of *E. gracilis* with the larvae of *D. latum* (Table X).

Table X

Cross geographical contacts of larvae of *D. latum* and adults of *E. gracilis*

Geographical region of		No. of specimens		Extens. of invasion %	Intens. of invasion
hosts	parasites	cont.	inv.		
Poland	Poland	223	145	65	6.0 (1-13)
Bay of Finland	Bay of Finland	72	70	97	8.2 (1-23)
Poland	Bay of Finland	158	102	64	3.8 (1-10)
Norway	Bay of Finland	64	36	56	3.2 (1-5)

In the first series of the experiments both partners from Poland were used. *E. gracilis* became invaded in a fairly high percentage; however, the observations of 33 adult individuals invaded and cultured individually indicate an irregularity of the development of the parasite, and when the populations become overdense (7 larvae), even the growth was inhibited (Guttow 1956). These results prove that *E. gracilis* does not fulfil in Poland the conditions of the obligatory host.

In the second series of the experiments the hosts and the parasites originated from the Leningrad environs. Here the extensiveness of invasion attained 97% and the development run a very regular course. The procercoids were formed in 12—14 days, and in the populations of various numerosity the appearance of the first procercoid took place at the same period of time. This proves that *E. gracilis* is the typical obligatory host of the procercoid of *D. latum* in the environs of Gulf of Finland.

The third series was based on the cross contact of *E. gracilis* from Poland with the larvae of *D. latum* from the environs of Gulf of Finland. As illustrated in the table X the extensiveness of invasion attained 64%, therefore it was close to that characteristic to the system *D. latum* — *E. gracilis* under the conditions of Poland. Observations showed a great irregularity of the speed of the development and of its course. And so, e. g. the populations consisting of 1—2 individuals, beside the slightly increased growth of the procercoid did not show any characteristics of their development. Other populations (7—10 individuals) possessed already on the 8th day following the inva-

sion 2 — 3 well formed proceroids. It seems that the course of the development runs with great individual deviations as if it were dependent on the individual characteristics and not on the species characteristics of the host.

The fourth series of the experiments was based on the cross contact of *E. gracilis* (from south Norway, lake Mjösa) with the larvae of *D. latum* from the environs of the Gulf of Finland. The experiments proved that the extensiveness of invasion attained barely 56%, the development of the proceroid run an irregular course as regards the speed of the growth and the formation of larvae in the separate invaded individual hosts. The period of the formation of the proceroids lasted on the average 12 — 18 days. In 8 cases it lasted above 20 days, whereby in not numerous populations often only single proceroids became mature.

Lower intensity of invasion and the disturbances of the speed and regularity of the development of the larvae in the hosts of the same species, but of various origin, suggest the possibility of the presence of certain local adaptations, evolutionally fixed between the host and the parasite occurring in the same terrain.

6. Comparison of data in the literature with the present findings

Numerous laboratory studies on the establishment of a list of *Copepoda* species susceptible to the invasion with *D. latum* give an opportunity to analyse the variability of the correlations between the two partners in various geographical zones. The proceroids of *D. latum* form parasitological systems with many species of *Cyclopoida* and *Calanoida*. The list of the hitherto investigated hosts species can be on the basis of the literature represented in the following way: (1) Hosts becoming easily invaded in the experiment, i. e., the potential natural hosts; (2) Hosts becoming invaded in a low percentage, and (3) Hosts not invaded (Table XI, XII, XIII).

As shown by the results of studies from various geographical zones, the *Calanoida* species are more susceptible to invasion with *D. latum*. Among the species of *Copepoda* easily invaded in the experiment there are 13 species of *Diaptomidae* and only 2 species of *Cyclopidae*.

The subfamily *Cyclopinae* with the typical representative, *C. strenuus strenuus*, includes among others a number of species, which up to 1927 were embraced by one name *Cyclops strenuus* s. lato. As shown by the studies of Michajłow et Wierzbicka 1935 and Guttowa 1956, each of the quoted species of the „strenuus group” is characterized by a peculiar reaction to the invasion with *D. latum*. Hence, the name *Cyclops strenuus* as the intermediate host of *D. latum* without the quotation of the author cannot be taken into consideration. The data reported in the past by Janicki et Rosen 1917 and other authors, who do not define more accurately the species, should be treated with great precaution. Therefore it seems probable that the host described by the name *Cyclops strenuus* is the lake species *Cyclops vicinus*, characterized by a high invasiveness and a rapid speed of development of the larvae.

Species of the subfamily *Cyclopinae* exhibit next to *Diaptomidae* the highest predestination to the invasion with *D. latum* in the juvenile or adult period, but not in all of them the development of the proceroid takes place. Numerous

Table XI

Copepoda species becoming easy invaded with *D. latum* in experiments

No.	Species	Author	Place of investigations	Distribution (Rylov 1930, 1948)
<i>Calanoida</i>				
1	<i>Eudiaptomus coeruleus</i> v. <i>vulgaris</i> (Schmeil)	Vogel 1930, Guttowa 1956	Germany, Poland	Europe, Central and North Asia
2	<i>Eudiaptomus gracilis</i> (Sars)	Janicki et Rosen 1917, Vogel 1930, Michajłow et Wierzbicka 1935, Morozova 1956, Guttowa 1956	Switzerland, Germany, Poland, Karelian SSR	North and Central Europe, Siberia
3	<i>Eudiaptomus graciloides</i> (Lill.)	Redlich 1925, Morozova 1957	Germany, Karelian SSR	North Europe, Siberia
4	<i>Acanthodiptomus denticornis</i> (Wierzejski)	Guttowa (present paper)	North Norway	Scandinavia, Alps, Carpathians, Turkestan, Tibet
5	<i>Diaptomus oregonensis</i> Lill.	Essex 1927	USA-Minnesota	North America
6	<i>Diaptomus sicilis</i> Forbes	Essex et Magath 1931	USA-Minnesota	"
7	<i>Diaptomus siciloides</i> Lill.	Essex et Magath 1931	USA-Minnesota	"
8	<i>Diaptomus piscinae</i> Forbes	Humes 1950	USA-Massachusetts	"
9	<i>Diaptomus sanguineus</i> Forbes	Humes 1950	"	"
10	<i>Diaptomus mississippiensis</i> Marsh.	Humes 1950	USA-Georgia	"
11	<i>Diaptomus albuquernensis</i> Herrich	Humes 1950	"	"
12	<i>Arctodiptomus ulomskyi</i> Tschetschuro	Utkina 1960	Ural	Ural
13	<i>Eurytemora affinis</i> (Pappe)	Humes 1950	USA-Massachusetts	North America
14	<i>Beckella minuta</i>	Beerup 1957	Australia	Australia
<i>Cyclopoida</i>				
1	<i>Cyclops strenuus strenuus</i> Fischer	Janicki et Rosen 1917, Vogel 1930, Morozova 1957	Switzerland, Germany, Karelian SSR	Europe, Asia, North Africa
2	<i>Cyclops furcifer</i> Claus	Guttowa (present paper)	Poland	Europe, Asia, North Africa
3	<i>Cyclops vicinus</i> Ulj.	Michajłow et Wierzbicka 1935, Guttowa (present paper)	Poland	North and Middle Europe

Table XII
Copepoda species becoming invaded weakly and sporadically with *D. latum*

No.	Species	Author	Place of investigations	Distribution (Rylov 1930, 1948)
	<i>Calanoida</i>			
1	<i>Eudiaptomus zachariasii</i> (Poppe)	Guttowa (present paper)	Poland, Bay of Finland	North and Middle Europe
2	<i>Diaptomus minutus</i> Lill.	Vergeer 1936	USA	-
3	<i>Gladiferens brevicornis</i>	Bearup 1957	Australia	-
	<i>Cyclopoida</i>			
1	<i>Eucyclops serrulatus</i> (Fischer)	Michajłow et Wierzbicka 1935, Bearup 1957	Poland, Australia	cosmopolitan
2	<i>Acanthocyclops vernalis v. robustus</i> (Sars)	Hall 1929, Essex 1927	USA	Europe, Asia, North America
3	<i>Mesocyclops oithonoides</i> (Sars)	Morozova 1957	Karelian SSR	Europe, Asia
4	<i>Mesocyclops leuckarti</i> (Claus)	Bearup 1957	Australia	cosmopolitan
5	<i>Tropocyclops prasinus</i> (Fischer)	Essex 1927	USA	Europe, Asia, North and South America
6	<i>Microcyclops varicans</i> (Sars)	Bearup 1957	Australia	cosmopolitan
7	<i>Cyclops strenuus strenuus</i> Fischer	Redlich 1925, Vogel 1930, Michajłow et Wierzbicka 1935, Guttowa 1956, Morozova 1957	Germany, Poland, Karelian SSR	Europe, Siberia, North Africa
8	<i>Cyclops lacustris</i> Sars	Guttowa (present paper)		North Europe
9	<i>Cyclops scutifer</i> Sars	Morozova 1957, Guttowa (present paper)	Karelian SSR, Norway	Europe, Siberia, North America
10	<i>Cyclops vicinus v. kikuchii</i> (Smirn)	Michajłow et Wierzbicka 1935, Guttowa (present paper)	Poland	North and Central Europe
11	<i>Cyclops insignis</i> Claus	Guttowa (present paper)	Poland, Bay of Finland	Europe

Table XIII
Copepoda species becoming not invaded with *D. latum* in experiment

No.	Species	Author	Place of investigations	Distribution (Rylov 1930, 1948)
Calanoida				
1	<i>Hemidiaptomus amblyodon</i> Marenz.	Guttowa (present paper)	Poland	Central and East Europe
2	<i>Diaptomus birghei</i> Marsh.	Humes 1950	USA	North America
Cyclopoida				
1	<i>Macrocylops albidus</i> (Jurine)	Redlich 1925, Esse 1927, Vogel 1930, Vergeer 1936, Guttowa 1956	Germany, Poland, USA	Europe, Asia, North Africa, North America
2	<i>Macrocylops distinctus</i> (Richard)	Bearup 1957, Guttowa (present paper)	Australia, Poland	Europe, Asia, North America, Australia
3	<i>Macrocylops fuscus</i> (Jurine)	Humes 1950, Guttowa 1956	USA, Poland	Europe, Asia, Japan, North Africa, North America
4	<i>Eucyclops serrulatus</i> (Fischer)	Redlich 1925, Esse 1927, Vogel 1930, Guttowa 1956	Germany, Poland, USA	cosmopolitan
5	<i>Eucyclops macrurus</i> (Sars)	Janicki et Rosen 1917, Guttowa 1956	Switzerland, Poland	Europe, West Asia, North Africa
6	<i>Eucyclops macruroides</i> (Lill.)	Guttowa 1956	Poland	Europe, Asia, North Africa
7	<i>Tropocylops prasinus</i> (Fischer)	Vergeer 1936	USA	Europe, North Asia, North and South America
8	<i>Acanthocylops vernalis</i> (Fischer)	Janicki et Rosen 1917, Guttowa 1956	Switzerland, Poland	Europe, Asia, North America
9	<i>Acanthocylops vernalis</i> v. <i>robustus</i> (Sars)	Vergeer 1936	USA	Europe, Asia, North America
10	<i>Acanthocylops americanus</i> Marsh.	Vergeer 1936	USA	North America
11	<i>Diacyclops bicuspidatus</i> (Claus)	Esse 1927, Vogel 1930, Michailow et Wierzbicka 1935, Vergeer 1936, Guttowa 1956	Poland, USA	Europe, Asia, North America
12	<i>Diacyclops bicuspidatus</i> v. <i>thomasi</i> Forbes	Humes 1950	USA	North America
13	<i>Megacyclops viridis</i> (Jurine)	Janicki et Rosen 1917, Redlich 1925, Vogel 1930, Guttowa 1956	Switzerland, Germany, Poland	Central and East Europe, Siberia
14	<i>Mesocylops leuckarti</i> (Claus)	Janicki et Rosen 1917, Esse 1927, Vergeer 1936, Guttowa 1956	Switzerland, Poland, USA	cosmopolitan
15	<i>Mesocylops oithonoides</i> (Sars)	Janicki et Rosen 1917, Guttowa 1956	Switzerland, Poland	Europe, Siberia
16	<i>Mesocylops dybowskii</i> (Lande)	Guttowa (present paper)	Bay of Finland	Europe, Asia, North Africa
17	<i>Paracyclops fimbriatus</i> (Fischer)	Esse 1927, Vergeer 1936	USA	cosmopolitan
18	<i>Ectocylops phaleratus</i> (Koch)	Vergeer 1936, Guttowa (present paper)	USA, Bay of Finland	cosmopolitan
19	<i>Cyclops abyssorum</i> Sars	Guttowa (present paper)	Poland	North Europe, North America

cases of degeneration of the larvae were observed by me exactly in this group. On the basis of these phenomena it can be concluded that the process of the adaptation of *D. latum* to its intermediate hosts in the first phase of the development is leading presently in the direction to overpower the family *Cyclopinae*.

All the remaining genera and species of the family *Cyclopidae* exhibit an almost complete resistance to the invasion with *D. latum*. The reports of several cases of invasion of *Eucyclops serrulatus* (Michajłow et Wierzbicka 1935), of *Thermocyclops oithonoides* (Morozova 1957), of *Mesocyclops leuckarti* (Bearup 1957), or of *Acanthocyclops vernalis* v. *robustus* (Hall 1929, Essex 1927) do not entitle to include those species to the circle of the intermediate hosts of *D. latum*. At present it is affirmed that the species of the families *Macrocyclopidae*, *Eucyclopidae*, *Acanthocyclopidae* and *Mesocyclopidae* do not play in the Baltic area any essential part in the developmental cycle of *D. latum*.

The analysis of the characteristics of the procercoids of *D. latum* discovered experimentally in various geographical zones displays a picture of the systems characteristic to Europe, North America and Australia.

In the areas of Europe bordering with the Baltic Sea there dominate *Eudiaptomus gracilis*, *E. graciloides*, *E. coeruleus* v. *vulgaris* and to a lesser degree *Cyclops vicinus*, *C. furcifer* and *C. lacustris*. They represent species characteristic to this geographical regions of the lake and small reservoir plankton, nowhere hitherto recorded except in the north and central Europe and western part of Siberia (Rylov 1930, 1948). In the course of my studies conducted in north Norway in the district of the lake Pasvik I achieved positive results of invasion in *Acanthodiaptomus denticornis*, a relics species of arctic origin, characteristic to mountaineous water bodies.

The second wide district of the occurrence of *D. latum* is in North America, in the environs of the lakes Portage, Elly, Winnipeg (Maga 1937). *D. latum* can form there under natural conditions systems becoming easily invaded in an experiment with several species of the family *Diaptomidae* as: *D. sanguineus* Forbes, *D. mississippiensis* Marsh., *D. silicis* Forbes, *D. silicoides* Lill. They are species typical to those terrains and are recorded nowhere else (Humes 1950).

D. latum transported with the movements of the human population to the various parts of the world, probably adapted itself relatively quickly to the new intermediate hosts of the group *Copepoda*. For instance, in Australia it was found that the common species of small lakes, *Beckella minuta*, becomes easily invaded. This species notwithstanding the high degree of the extensiveness and intensity of invasion in the experiment can play a part of the obligatory host of the procercoids of *D. latum* in this geographical region (Bearup 1957).

As shown by this analysis, the adaptation of the parasite to the first intermediate hosts leads in the direction of overpowering the typical species, most widely occurring in a given area and ecologically connected with the parasite.

7. Discussion

The fundamental characteristics, which should be submitted to analysis when an attempt is made to define a species as the host, are the extensiveness and intensity of invasion and the speed of the development of the larvae in the body cavity. Beside the classification of the groups of hosts elaborated on the basis of the previously described criteria by Michajłow 1932, there are in the literature interesting conceptions of the forms of the relations between the parasite and the host, presented by Davtian et Šulc 1954, and Kisielewska 1959. Kisielewska presents her classification from the physiological and ecological point of view and discerns 4 systems: obligatory, auxiliary, accidental and apparent. The obligatory system, resulting from physiological connections, corresponds to the obligatory system of Davtian et Šulc 1954. The auxiliary and accidental systems are two terms corresponding to the III and IV groups of Michajłow's classification and to the facultative and abortive systems of Davtian et Šulc. Both the systems result from physiological and ecological connections. Kisielewska introduced the term apparent system which is formed when the parasite reaching the body cavity dies there. It is affirmed that both the systems and the groups of hosts are reliable to variabilities, which can be caused by ecological, geographical and other factors. Such a classification was also accepted by Michajłow 1959.

In the materials elaborated by me in the present investigations there emerge three types of systems analogous to the types of systems presented by Davtian et Šulc 1954 and by Kisielewska 1959. The obligatory system in Poland can be formed with *Eudiaptomus coeruleus* v. *vulgaris* and *E. gracilis* in the phase of the copepodid. The typical auxiliary system is formed with the species of the group of auxiliary hosts: *Cyclops vicinus*, *C. furcifer* and *C. strenuus strenuus* in the phase of the copepodid. The accidental hosts can form systems of the accidental and apparent types, because I found cases of dying out and inhibition of the development of the larvae in the body cavity exclusively in this group.

In Poland, *Eudiaptomus gracilis* can form with *D. latum* systems of various types. The development and the relations in the populations of the procercoids in every individual host appear differently (mosaic picture of the development of the population, Fig. 2), therefore almost every individual of *E. gracilis* can give with the larvae of *D. latum* an example of a different type of a system.

The classification of the systems parasite — host is characterized by a more profound approach to the problem, because it includes the wholeness of the mutual connections between the parasite and host, as the manifestations of the resistance of the host and the degree of the adaptation of the parasite. Due to this it is more concrete. Because the types of the systems are terms strictly connected with the parasite and its host group, they cannot form a general pattern to many phenomena of the parasitism. The classification of the hosts corresponds fundamentally with the types of the systems, but it offers greater possibilities to take into consideration also the ecological and geographical factors. Thanks to the more general approach, I think, the classification of hosts can be applied generally to every helminthological group and to every section of the life cycle of the parasites.

The classification of the hosts and systems has its value only in connection with certain definite conditions, it cannot be comprehended in an absolute way. The systems and hosts are subject to variabilities as shown by laboratory studies in connection with the geographical zones, as well as with the kind of the water bodies.

As shown by observations, certain shifts in the formation of the types of the systems can be caused also by phenological factors (Kisielewska 1957); however in my material I could not observe major differences caused by them. Vogel 1930 suggests that there can be a possibility of the influence of the character of the water reservoirs mainly that of its pH on the change of the resistance of the hosts living in them. As an example he quotes a lack of invasion of *Cyclops strenuus* from rural ponds contaminated with detritus, and numerous cases of the copepods of this species originating from other water reservoirs being invaded.

Stronger invasion of young individuals of *Cyclops strenuus strenuus* can suggest that there may be an increase of the resistance connected with the age.

A serious factor influencing the formation and the evolutionary development of the systems is the geographical factor. There are data proving that a different part is played by the same species of hosts to the same species of parasites in various geographical regions, e. g. species playing the main role of the first intermediate hosts of *D. latum* in one geographical region are replaced by other species in other regions. This phenomenon recalls an analogy to the phenomenon known in the zoogeography and defined by the term vicariate and deserves the term parasitological vicariate. It is not limited to the tapeworms and their larvae. A change of roles between the species of hosts dependent on the geographical region is signalized by Benex and Lamy 1959 in the regional races of the intermediate host of *Schistosoma mansoni* — *Australorbis glabratus*, which in Brasil and Puerto Rico shows a difference in reaction to the invasion by the parasite. This phenomenon suggests a possibility of the presence among the hosts and parasites of certain regional races of certain differences, may be of mainly physiological character.

This conclusion is supported by the results of the experiments with the geographical cross contact between the parasite and host, described by me, particularly by the fact that *Eudiaptomus gracilis*, which forms the obligatory system in the environs of the Gulf of Finland, has in Poland and Norway a system of the auxiliary system characteristics.

Eudiaptomus gracilis may in various geographical regions and in various geographical conditions undergo changes caused by local agents (climatological, chemical, phenological). Such changes may become fixed in the process of evolution. In connection with this, the species may represent a different value as the host to the procercoids of *D. latum* in the various geographical regions. These observations throw light on the problems of the specificity. It seems that the specificity of *D. latum* as regards its first intermediate hosts has a physiological character. It is conditioned by the metabolism of the host, indicated by the stronger disposition to invasion of the species of the family *Diaptomidae* than *Cyclopidae*, females than males, younger than older individuals. The differences in the invasion during the geographical cross contact of the parasites and hosts affirm also the ecological character

of this specificity, sufficiently broad and conditioned by the alimentary regime, which creates the chance of invasion.

Summarizing these considerations the conclusion can be drawn that the studies of the parasite — host relations in the first phase of the development of *D. latum* should be conducted in close connection with the definite region. All summary classifications based on a mixed material do not reproduce the real picture and do not reflect the actual relations between the parasite and the host. However, the determination of these relations for a given region, for given conditions and the comparison of the data referring to various regions may reproduce to a certain degree the picture of reality prevailing in the nature.

Summary

The authoress studied three problems connected with the formation of the system parasite — host: (1) The influence of the external environment on the embryonic development, vitality and invasiveness of the coracidia; (2) The relationship in the populations of proceroids in various types of systems; (3) The occurrence of hosts of the proceroids of *D. latum* among *Copepoda* in Poland and in some other countries of the Baltic region, the classification of those hosts and the variability of their properties depending on the geographical and ecological factors.

On the basis of experiments she states that the temperature is the most important factor acting in the period of the embryonic development. The development of the eggs may take place at the temperature of 8—35°C, below 8°C it is inhibited and at 35°C the eggs die. The invasiveness of the larvae appears at the moment of the hatching and persists till the larvae sink to the bottom (36—48 hours). The temperature of the environment in which the eggs are located influences the time of the invasiveness of the larvae.

The development of proceroids of *D. latum* in the obligatory host at the temperature of 18—20°C lasts about 14 days. Between the 8th and 12th day the cercomer is formed. The development of a not overdense population of the proceroids in the obligatory host is uniform as regards the growth of the individuals and the rate of their maturation. Under conditions of over-density there appears a differentiation of the population expressed by a subdivision of the individuals into a group leading in the development, a delayed group, and a group completely inhibited in its growth and development. The greatest differences in the growth of the individual larvae occur between the 8th and 12th day of the development when the population enters into the period of the formation of the proceroids. The cause of the differentiation under the conditions of over-density is most likely the food deficiency. The cases of disturbances of the development in not overdense populations in the system of the auxiliary type can be explained by an inadequate mutual adaptation between the host and parasite. In the body cavity of accidental hosts the phenomenon of the dying out, delay, or complete inhibition of the development of the larvae can be observed. These phenomena result not from the intrapopulation relations because their source is rather the absence of a physiological and evolutionary adaptation of both components of the system of the accidental type.

Among Copepoda in Poland, to the invasion were susceptible: *Eudiaptomus coeruleus* v. *vulgaris*, *E. gracilis*, *E. zachariasii*, *Cyclops strenuus strenuus*, (copepodids), *C. vicinus*, *C. vicinus* v. *kikuchii* and *C. furcifer*. Among those species the conditions of the obligatory hosts (high extensiveness and intensity of invasion, the most rapid rate of development of larvae in the body cavity) are fulfilled by *E. coeruleus* v. *vulgaris* and *E. gracilis*, in the copepodid phase. The auxiliary hosts are: adult *E. gracilis*, *C. vicinus*, *C. furcifer*, adult *C. strenuus strenuus*, *C. insignis* and *Eudiaptomus zachariasii*. The obligatory hosts of the procercoid of *D. latum* in the area of the Gulf of Finland are: *E. gracilis* and *E. graciloides* and in Norway: *Acanthodiptomus denticornis* and *E. gracilis* — copepodids. The list of the hosts of the procercoids of *D. latum* in Poland, Norway and in the area of the Gulf of Finland shows certain differences. At the cross contact of the parasite from one region and the hosts from other regions there appear differences in the extensiveness and intensity of invasion and disturbances in the speed and regularity of the development of the larvae in hosts of the same species, but of various geographical origin. This phenomenon proves the existence of certain local connections between the host and parasite.

On the whole, Calanoida constitute a group more disposed to invasion than Cyclopoida. Among Cyclopoida a particular place is occupied by the subfamily Cyclopinae. Numerous representatives of this subfamily show a susceptibility to the invasion in the juvenile and adult period. The families: *Macrocyclopidae*, *Eucyclopidae*, *Acanthocyclopidae*, *Mesocyclopidae* do not play any part in the Baltic region in the developmental cycle of *D. latum*.

On the basis of the data in the literature and personal findings the author draws the conclusion that in various geographical and ecological conditions the different species of Copepoda can play a part of the obligatory intermediate hosts of *D. latum*.

Author's address:
Zakład Parazytologii P.A.N.
Warszawa, Pasteura 3

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STRESZCZENIE

Autorka rozpatruje trzy zagadnienia związane z powstawaniem układu pasożyt — żywicieli: 1. Wpływ środowiska zewnętrznego na rozwój embrionalny oraz żywotność i inwazyjność koracydiów; 2. Stosunki w populacjach procerkoidów w układach różnego typu; 3. Występowanie żywicieli procerkoidów *D. latum* wśród widłonogów Polski i niektórych innych krajów w strefie Bałtyku, oraz klasyfikacja tych żywicieli i zmienność ich właściwości w zależności od czynników geograficznych i ekologicznych.

Na podstawie doświadczeń stwierdzono, iż temperatura jest najważniejszym czynnikiem działającym w okresie rozwoju embrionalnego, i że inwazyjność koracydiów występuje od chwili wylęgu do chwili opadnięcia larwy na dno. Temperatura środowiska, w którym przebywają jaja, wpływa na czas trwania zdolności inwazyjnych larw.

Rozwój nieprzegęszczonej populacji procerkoidów w żywicielu właściwym jest równomierny pod względem wzrostu osobników i tempa ich dojrzewania. W warunkach przegęszczenia następuje różnicowanie się populacji na grupę przodującą w rozwoju, opóźniającą się, oraz całkowicie zahamowaną we wzroście i rozwoju.

Wśród widłonogów z Polski zarażeniu ulegały: *Eudiaptomus coeruleus* v. *vulgaris*, *E. gracilis*, *E. zacharias*, *Cyclops strenuus strenuus* (kopepodity), *C. vicinus*, *C. vicinus* v. *kikuchii* i *C. furcifer*. Spośród tych gatunków warunki żywicieli właściwych spełniają *E. coeruleus* v. *vulgaris* oraz *E. gracilis* w fazie kopepoditu. Żywicielami pomocniczymi są *E. gracilis* dorosłe, *C. vicinus*, *C. insignis* i *E. zacharias*.

Właściwymi żywicielami procerkoida *D. latum* z wybrzeża Zatoki Fińskiej są *E. gracilis* i *E. graciloides*, a w Norwegii *Acanthodiptomus denticornis* i *E. gracilis* — kopepodity.

Na ogół *Calanoida* stanowią grupę bardziej skłonną do zarażenia niż *Cyclopoida*. Wśród *Cyclopoida* szczególne miejsce zajmuje podrodzina *Cyclopinae*, której stosunkowo liczni przedstawiciele wykazują skłonność do zarażenia się w okresie dojrzałym lub młodocianym. Rodziny: *Macrocyclopidae*, *Eucyclopidae*, *Acanthocyclopidae*, *Mesocyclopidae* w rejonie bałtyckim nie grają roli w cyklu rozwojowym *D. latum*.

Z danych z literatury oraz badań własnych autorka wysuwa wniosek, że w różnych warunkach geograficznych i ekologicznych odmienne gatunki *Copepoda* mogą spełniać rolę właściwych żywicieli pośrednich *D. latum*. Zjawisko to nazywa wikariatem parazytologicznym.